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EMIGRATION RESPONSE BEHAVIOR: II: THE RESPONSES OF *DROSOPHILA BUSCKII* (DIPTERA: DROSOPHILIDAE)[1]

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The movement of members of a population from one geographic locality to another is an important factor in the evolutionary process. It is clear that not all members of a given population emigrate. Of those members which do move, some are compelled by genetic factors, some by environmental factors and some by the interaction of both. While emigrants must be capable of surviving and reproducing in the new localities, fine level adaptations to a new area evolve only *after* arrival. Thus, the possibility of extending the range of a species depends on the ability of the genetic architecture of the emigrants to respond to a new environment in addition to their propensity to move from an old one. It follows that the examination of genetic and environmental factors influencing movement from one locality to another is of prime importance to evolutionary and behavioral biology.

This is a report from an ongoing study that is examining the *interacting effects of genotypes and environments* on the movement of *Drosophila* from their place of origin to new locations. The active change in location of members of a population results from two distinguishable processes, namely, migration and dispersal. While these terms have had various meanings, Rockwell et al. (1978) encouraged the use of the following definitions: *Migration*—the goal oriented movement of a fraction of the population; *Dispersal*—the movement of a fraction of a population as a result of the general (random) activity of its members. The overall movement of organisms from their place of origin to a new location is termed *emigration response behavior*.

Emigration response behavior of *Drosophila* has been examined in the laboratory by a number of researchers who have used a system devised by Sakai et al. (1958). That system consists of a set of four interconnected vials through which individual flies can move (Fig. 1). Emigration response behavior is measured as the number (or percentage) of individuals leaving the central vial. Rockwell et al. (1978) pointed out that this single measurement of emigration response confounds migration and dispersal. They proposed that by measuring emigration responses in the Sakai system relative to four specific environmental configurations, one could obtain a clearer view of the relative contributions of migration and dispersal to the overall emigration response behavior of a species (or strain).

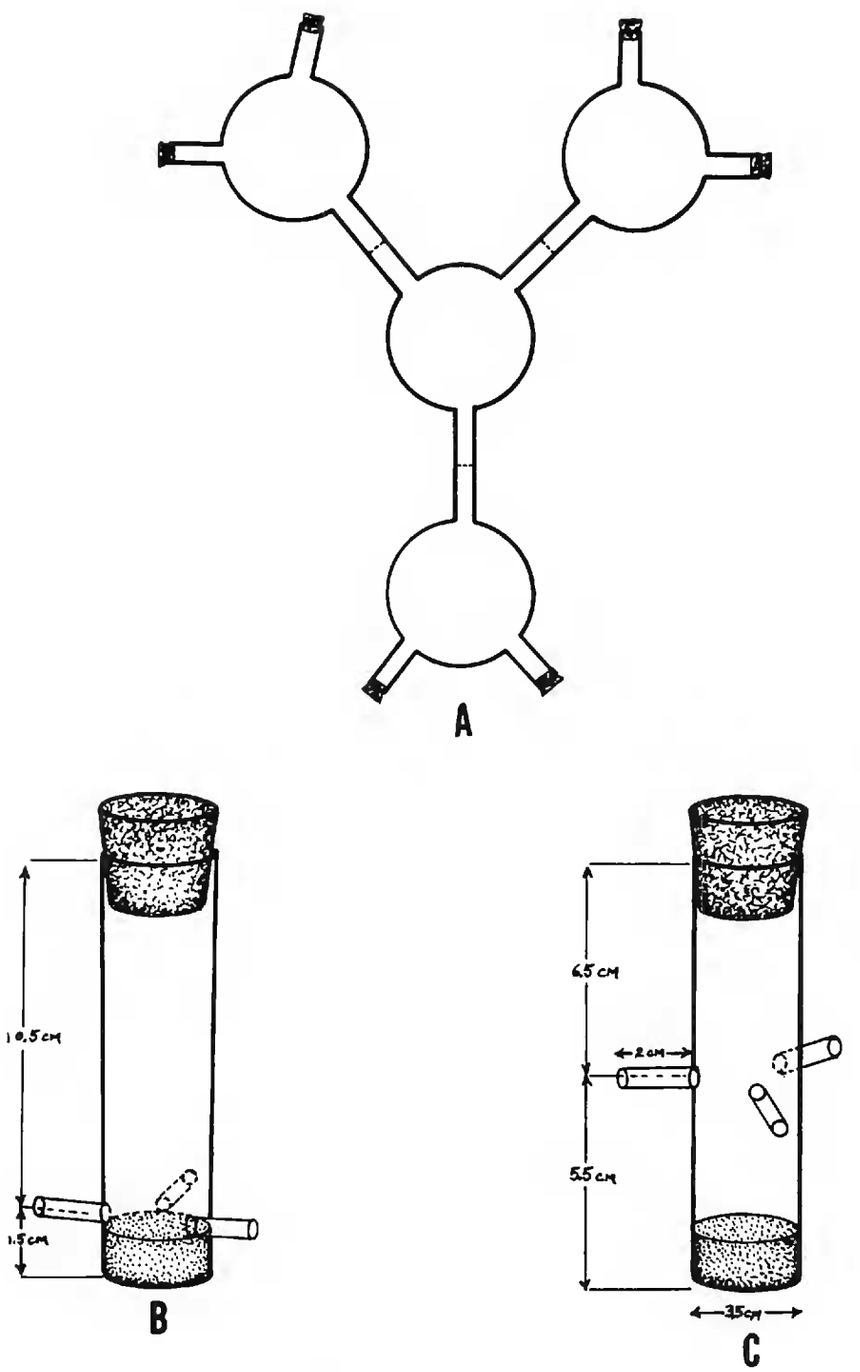

Fig. 1. The emigration response behavior apparatus modeled after Sakai et al. (1958). A—the arrangement of vials; B—low vial; C—high vial.

The specific environmental configurations are the four possible combinations of two levels of each of two factors, namely *height* of the connecting tubes and *lighting condition*. The original Sakai system utilizes connecting tubes which are about 4 cm above the level of the food surface in the vials (Fig. 1C). As such, passage from the central vial to the three peripheral vials can be viewed as three-dimensional; that is, requiring movement through a volume. The use of vials whose connecting tubes are at the same level as the food surface changes this to two-dimensional movement involving only

area. If the passage of flies through this system contains a general activity component, one would expect substantially more emigration in the vials with the low connecting tubes simply because the flies would have more chance, in a fixed time period, to encounter the connecting tubes. Thus, the greater the difference between the emigration responses measured in the two types of vials (high versus low), the greater is the dispersal component of the overall emigration response behavior.

The role of light as a stimulus that increases general activity in *Drosophila* has been extensively noted (Grossfield, 1971). If light plays this role in the Sakai system and if the passage of flies through this system contains a general activity component, one would expect substantially more emigration in the light than in the dark. Thus, the greater the difference between the emigration responses measured in the light versus dark, the greater the dispersal component of the overall emigration response behavior.

The present paper focuses on the emigration response behavior of *Drosophila busckii*. This species, like *D. melanogaster* has a global distribution. However, there is a phylogenetic peculiarity of the genus in that it is the only member of its subgenus *dorsilopha* (Throckmorton, 1975). In addition, *D. busckii* possesses an inordinately low level of genic variation (and, hence, heterozygosity) which contrasts it not only with the rest of the genus but with many other organisms (Prakash, 1973). The inclusion of this species in the overall study of the interacting effects of genotype and environment on the movement of *Drosophila* from one locality to another is especially important for two reasons. First, because of the taxonomic and genetic distinctness of this species in the genus, the evaluation of its emigration response behavior will provide information on the general applicability of this experimental system, and the conclusions reached using it, to studies of interlocality movement in the genus.

Second, because of the low heterozygosity of *D. busckii,* the extent to which the emigration response changes across the four environmental configurations will provide important information on the general relationship between behavioral plasticity (i.e., flexibility) and genetic architecture. While it is widely held that the level of plasticity of a given behavioral trait is related to underlying genetic architecture such as the level of heterozygosity (Dobzhansky, 1973), most studies on the nature of that relationship have only used species that are quite heterozygous in nature (Caspari, 1967; Rockwell et al., 1975).

Methods and Materials

Stocks and Culturing

The strain of *Drosophila busckii* used in these experiments was collected at Wyeth Farm, Glenburnie, Ontario, in the fall of 1975. Since that time, it

has been maintained as a mass culture in ½ pint bottles on a medium composed of equal volumes of instant mashed potatoes and water (Tegosept® is added to reduce mold contamination). The stock is maintained at 20.0°C, 85% relative humidity and constant illumination.

Equipment

The migration vials are modeled after those of Sakai et al. (1958) and are depicted in Figure 1. Two types of vials were used:

a) *high vials* (Fig. 1C) in which the connecting tubes are 4.0 cm above the surface of the medium;
b) *low vials* (Fig. 1B) in which the connecting tubes are at the same level as the surface of the medium.

As depicted in Figure 1A, four high vials or four low vials were connected with clear tape to form a single migration system. The unused connecting tubes of the three peripheral vials were plugged with corks. A mixture of instant mashed potatoes and water (1:1) was used as the medium. The systems were assembled one hour before the beginning of experimental trials. Each assembled system was placed in an open plastic tray measuring 28 × 28 × 16 cm high. The inside of each of these trays had been painted white and the outside had been painted black. The painting of the trays served to eliminate extraneous visual cues and to provide diffuse uniform illumination. The trays containing the migration systems were placed in a 20.0°C environmental chamber.

Procedure

Flies were collected daily from replicate culture bottles and batches of 20 males and 20 females were placed together in 8 dram food vials. These were stored in an incubator at 20.0°C, 85% relative humidity and constant illumination. A set of 50 males between 7 and 10 days old was randomly collected from these vials and placed in an empty 8 dram vial for 30 minutes. Humidified CO_2 was used as the anesthesia for these procedures.

A given set of 50 males was aspirated into the central vial of either a high or a low migration system. If the system was to be tested in the dark, the tray containing the system (and the flies) was immediately covered with black cloth. Preliminary studies demonstrated that no light entered such trays. If the system was to be tested in the light, the tray containing the system was placed beneath a fluorescent light fixture (consisting of two 40 watt tubes suspended 24 inches above the tray).

After inserting the flies and placing the trays in the appropriate lighting condition, the system was left undisturbed for 24 hours (until 1000 hours on the following day). At that time, the number of flies in the three peripheral

vials was determined. The total number of flies in the three peripheral vials was used as the measure of *emigration response* for a given configuration. The measure can range from 0 to 50.

Experimental Design and Statistical Procedures

In order to examine the relationship between height and lighting condition, the experiments were performed in a factorial fashion. Three replicates of each combination of the levels of the two factors were performed in a randomized blocks fashion. Preliminary analysis of the data demonstrated no effects of blocks, so the replicate sources of variation were pooled (Winer, 1971). The data were then analyzed with factorial analysis of variance. The factorial design and analysis were used to assess whether the factors affect the emigration response behavior and to determine whether the two factors interact.

The emigration responses of *D. busckii* were compared to those of *D. melanogaster* with factorial analysis of variance. The emigration responses of *D. melanogaster* used in that comparison were measured under conditions identical to those just described and formed a part of a study reported in Rockwell et al. (1978).

Results

The emigration responses of male *D. busckii* in the four environmental configurations are given in Table 1 as means with their associated standard errors. The responses were analyzed with factorial analysis of variance and the results of that analysis are summarized in Table 2. There is a highly significant effect of tube height overall; the emigration response is greater in the low tubes. There is no significant effect of lighting condition on the emigration response. Importantly, there is no significant interaction between tube height and lighting condition; tube height modulates the response equivalently in both the light and the dark.

The emigration responses of *D. busckii* were compared to those of *D.*

Table 1. The emigration response behavior of male *Drosophila busckii* measured in the four conditions of the Sakai system.

Lighting condition	Tube height	
	Low	High
Constant light	31.33 ± 1.76	20.33 ± 2.33
Constant dark	36.33 ± 4.70	19.33 ± 2.84

NB: ±Standard errors.

Table 2. Analysis of variance of the emigration response behavior of male *Drosophila busckii*.

Source of variation	Degrees of freedom	Mean square
Tube height (H)	1	588.00[2]
Lighting condition (L)	1	12.00
H × L	1	27.00
Error	8	29.08

NB: All sources were tested over the error term.
[2] Significant at the 0.01 level of probability.

melanogaster using the three factor analysis of variance summarized in Table 3. Examining the main effects first, it is clear that there is no *overall* difference between the two species. That is, the emigration response behaviors of the two species, *averaged across the four environmental configurations,* do not differ significantly. In sharp contrast, the overall emigration responses for the two tube heights, averaged across lighting conditions and species, are quite significantly different. The emigration response in the low tubes is twice that in the high tubes (34.15 versus 16.99). The overall emigration responses for the two lighting conditions, averaged across tube height and species, are significantly different. The emigration response in the dark is greater than that in the light (28.57 versus 22.57).

Of crucial importance is the highly significant three-way interaction between tube height, lighting condition and species. Given the simultaneous

Table 3. Analysis of variance of the emigration response behavior of male *Drosophila busckii* and *D. melanogaster*.

Source of variation	Degrees of freedom	Mean square
Tube height (H)	1	1768.17[2]
Lighting condition (L)	1	216.00[3]
Species (S)	1	37.50
H × L	1	216.00[3]
H × S	1	60.16
L × S	1	96.00
H × L × S	1	486.00[2]
Error	16	44.99

NB: All sources were tested over the error term.
[2] Significant at the 0.01 level of probability.
[3] Significant at the 0.05 level of probability.

occurrence of a significant interaction between tube height and lighting condition and the lack of any significant interaction between tube height and species, the three-way interaction may reasonably be interpreted as a nonadditive effect between the two species for the tube height by lighting condition interaction. That is, the interrelationship between tube height and lighting condition, in their joint effect on emigration response, differs between the two species.

This interpretation is further supported by comparing the separate analyses of tube height and lighting condition effects for the two species. In the factorial analysis of tube height and lighting condition effects on the emigration response behavior of male *D. melanogaster* (Rockwell et al., 1978), it was shown that the tube height by lighting condition interaction is highly significant. For *D. melanogaster,* then, the effects of tube height and lighting condition are not independent; tube height modulates the response differentially with light. Recalling the analysis summarized in Table 2, tube height modulates the emigration response of *D. busckii* equivalently in the light and in the dark. Thus, the interdependence of tube height and lighting condition on the emigration response behavior of these two species is different.

Discussion and Conclusions

It is clear that tube height modulates the emigration response behavior of *Drosophila busckii.* The greater emigration response displayed in the low tubes is consistent with the existence of a general activity component in the overall emigration response behavior of this species. As explained earlier, such a component would be expected to result in more two-dimensional movement than three-dimensional movement.

There is no apparent effect of lighting condition on the emigration response behavior of this species; the emigration response is the same in constant light and constant dark. This result is not in agreement with the accentuating effect of light on general activity widely noted for *Drosophila* (Carpenter, 1905; Manning, 1965). This difference may reflect a peculiarity of the overall general activity behavior of *D. busckii.* It may also reflect the existence of several general activity programs in this species, each of which may serve as a component of different overall behavior systems. While the latter explanation is consistent with the results of experiments with *D. melanogaster,* this entire question is still under investigation.

In general the emigration response behavior of *D. busckii* measured in the Sakai system is a composite of both dispersal and migration components. In that sense, the overall emigration response is like that of *D. melanogaster.* It is clear, however, that *only* by assessing the emigration responses under the four environmental configurations can the *underlying nature* of the emigration response behavior be ascertained for either species. As will

be discussed below, it is this underlying nature which is crucial for interspecific comparisons.

These two species do not differ significantly in their emigration response behaviors averaged across the four environmental configurations. While interspecific differences can be shown for the emigration response measured in specific configurations (e.g., *D. melanogaster* has a greater response than *D. busckii* for the high tubes in the dark), the crucial difference between these species derives from the comparison of the response spectra of their emigration response behaviors. The *response spectrum* of a behavior is the plasticity of the measured behavioral response with respect to specified environmental perturbations. Behavioral plasticity is the tendency of a behavioral phenotype to change in form or intensity in response to alterations in the environment. Such plasticity reflects the norm of reaction of the genetic system underlying the behavior in question (Dobzhansky, 1970). Rockwell and Seiger (1973) pointed out that the response spectrum of a given behavior is most important in research directed at the elucidation of the underlying mechanisms or evolutionary significance of a given behavior.

The emigration response behavior of *D. busckii* is plastic with respect to tube height but not with respect to lighting condition. The emigration response behavior of *D. melanogaster* is plastic with respect to both tube height and lighting condtion. Considering the four environmental configurations, then, it appears that the emigration response behavior of *D. busckii* is less plastic than that of *D. melanogaster*. It follows that with respect to these environmental perturbations, the norm of reaction of *D. busckii* is narrower than that of *D. melanogaster* for emigration response behavior. Considering the joint effects of the two factors on the response, it also appears that the plasticity (and, hence, norm of reaction) of *D. busckii* is less complex. It will be recalled that in *D. busckii* the effects of tube height were independent of lighting condition. In *D. melanogaster,* the effect of tube height was modulated by lighting condition.

Overall the norm of reaction of *D. busckii* appears to be narrower and less complex than that of *D. melanogaster* for this behavior. There is no doubt that such differences in plasticity and norm of reaction are related to differences in genetic architecture between these two species. The results presented here are consistent with the possibility that the reduced plasticity of this behavior in *D. busckii* derives directly from the reduced heterozygosity of this species. Formal demonstration of that specific relationship awaits further investigation.

Since plasticity is, in general, a product of the genetic architecture underlying a given behavioral trait, the level of plasticity must ultimately derive from the evolutionary history and ecological requirements of a species. Similarly, interspecific differences in plasticity must derive from interspecific differences in these two factors. In fact, a portion of interspecific dif-

ferences in genetic architecture (and plasticity) may reflect the action of selection directed at the level of behavioral plasticity itself (Emlen, 1973; Rockwell and Cooke, 1977). It is tempting to relate the differences in plasticity demonstrated in this work to differences in the evolutionary histories and ecologies of these two species. Such speculation, however, must await further clarification of the evolutionary role of dispersal and migration in this genus. It is clear from this work that studies attempting such clarification must consider the plasticity and, hence, the norm of reaction of emigration response behavior to be at least as important as the overall mean behavior.

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Footnote

[1] Contribution 2 from the Theoretical Biology Study Group at City College of New York.

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SCIENTIFIC NOTE

SYNONYMY OF THE GENUS *EUPLUSIA* MOURE UNDER *EUFRIESIA* COCKERELL (HYMENOPTERA, APIDAE, EUGLOSSINI)

The genus *Eufriesia* was originally based on the single species, *pulchra*. Subsequently, another species, *lucifera* Kimsey, was added. It was distinguished from the genus *Euplusia* by the broad flat scutellum, entire head and T-III-VI or VIII brightly metallic with erect yellow setae, and the rest of the body black with black setae.

On comparison of male genitalia of *Eufriesia pulchra* (F. Smith) and *lucifera* Kimsey with the male genitalia of *Euplusia* species, I find no differences to support the separation of these two genera. Unlike other Euglossini, both of these "genera" have strongly bilobed gonostyli and trilobed gonocoxae.

Many external characteristics are also remarkably similar. Examination of the entire genus *Euplusia* reveals a number of species with the same color pattern as *Eufriesia,* including *formosa* (Mocsáry) and *theresiae* (Mocsáry) and other species with a broad flat scutellum, including *violacea* (Blanchard) and *chalybaea* (Friese). The genera share the following external characteristics, which distinguish them from all other euglossines: male hindtibial slit reaching apex; male midtibia with two adjacent felty patches; face brightly metallic without white maculations, and female with a corbicula.

The differences between these two groups are of species value only. *Eufriesia pulchra* and *lucifera* actually appear to belong to a species group containing four species of *Euplusia*.

The genus *Eufriesia* described by Cockerell (1908) has priority over *Euplusia* Moure (1943) which was a replacement for the preoccupied *Plusia* Hoffmannsegg (1817).

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